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ECOSYSTEM MODELLING IN THE MARINE ECOSYSTEMS DIVISION
A STATUS REPORT*

by

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BACKGROUND

Ecosystem modelling in the Marine Ecosystems Division (MED) was a natural outgrowth of the development of multispecies approaches to fishery management begun at NEFC more than a decade ago (Grosslein, Brown and Hennemuth, 1979). Since its establishment in 1977 the Ecosystem Dynamics Investigation has been investigating various holistic approaches to fisheries problems within the framework of the total ecosystem, and has developed several conceptual models as well as some analytical and simulation models.

An initial step was the estimation of production and consumption by the finfish biomass on Georges Bank based on an energy balance equation (Grosslein et al., 1980) The next step was to construct an energy budget for Georges Bank. This provided for the first time quantitative estimates of production of the lower trophic levels with implications for fish production (Cohen et al., 1982). This approach has since been expanded to consider the magnitude of predation by adult fish on sub-adult fish and the production of pre-exploitable fish (Cohen and Grosslein, 1982; Sissenwine, Cohen and Grosslein, 1984). The energy budget approach has been carried to its conclusion in the chapter on total productivity for the book on Georges Bank (Cohen and Grosslein, in press) where all trophic levels from phytoplankton to apex predators have been included. The chapter attempts to construct a quantitative picture of the way energy is produced and utilized on Georges Bank and compares it with other well-studied shelf ecosystems. This will help establish the most fruitful lines of investigation for future field, laboratory and modelling studies. The energy budget has provided a valuable quantitative framework for understanding the limits to fish production on Georges Bank. It has also yielded major new insights into the critical recruitment process in fishes. Work on the energy budget has involved many NEFC scientists and synthesis of a large data base within the MED as well as other divisions, and has required frequent updating of estimates. Thus, it has taken a lot of time, particularly for personnel in the Ecosystem Dynamics Investigation. Concurrent with these activities, personnel the Ecosystem Dynamics Investigation were also carrying out work with the physical oceanographers on the nitrogen balance in the Gulf of Maine and on Georges Bank (Schlitz and Cohen, 1984) and the role of advection on phytoplankton, zooplankton and ichthyoplankton (Mountain and Cohen, 1982; Cohen et al., 1982).

Concurrent with work on the energy budget we have been developing a multispecies fishery research and management model called GEORGE (Hahm, 1983). Following a lengthy period of evaluating candidate models and approaches (involving several workshops including one at Harvard with Bossert, and extensive review of other models especially DYNUMES by Lavaestu), it was decided to construct our own model along the lines of the Andersen-Ursin model (Andersen and Ursin, 1977). Due to constraints on hiring we were unable to recruit an experienced modeler and obtained a graduate student (Wendell Hahm) to begin construction of the model, and initiated training in modelling for Ed Cohen.

GEORGE is a simulation model designed to help evaluate the natural biological and physical controls over fish production and for predicting long-term effects of various management strategies. Major emphasis has been on evaluating multispecies predator-prey interactions among adult and juvenile fishes since it has become apparent that predation on juvenile fishes is a key factor controlling recruitment variability. A great deal of effort has gone into evaluating the food habits data base and developing size selective feeding and electivity functions. We have patterned the feeding function after Andersen and Ursin (1977). We have worked closely with Ursin on the problem of electivity of predators for specific prey as well as the digestion and growth rates of fish in general. Hahm and Langton (1980) summarized prey size selection for major fish species of Georges Bank in a form which could be used in predator-prey simulations. We have worked with Ursin to refine these coefficients, and are completing two papers on these problems, a general digestion rate model for field caught fish (Pennington, to be submitted) and a comparison of the feeding and growth of cod from Georges Bank and other North Atlantic stocks (Ursin et al., to be submitted). Additional work that bears directly on the precision of input data for the model is that of Pennington on the statistical properties of MARMAP ichthyoplankton and trawl survey data (Pennington, 1981; Pennington, 1983) although Hahm completed the construction of GEORGE and made preliminary debugging runs we have had problems in validating the present form of the model against the available data. The model is unstable and crashes within a year. While some of this instability may be due to the input data on feeding rates, the problem is also due to the coding of the model. The processes of growth, feeding and mortality are carried out consecutively rather than simultaneously, and the order of execution influences the model results. In order to properly de-bug the model it will have to be taken apart and re-coded. The task of re-coding GEORGE or constructing an alternative model (in either case the same basic types of equations will be used) for evaluating management related problems, should now be transferred to the Resource Assessment Division (RAD). RAD has the expertise for this, and the problem of modelling the recruitment process alone (i.e. factors controlling year-class success) will require the full resources of the MED.

Although the concept of GEORGE is still valid, it is a large scale multi-purpose model of the ecosystem and is probably premature for the level of understanding we have of the ecological processes controlling production and variability in the ecosystem. Energy budget calculations are adequate for insight into gross patterns, but they are not sufficient as a basis for simulation of ecosystem dynamics. Recruitment in fish populations is the single most important process in the field of fishery ecology and until we clarify the factors controlling variability in recruitment, especially the role of predation mortality on young fish, we won't have a valid mechanistic basis for linking recruitment to lower trophic levels and the physical environment, or for predicting effects of various harvest strategies. This view was shared by the majority of modelers at the recent special workshop on application of ecosystem models to fishery management (see report Panel A in Turgeon, 1983). For the above reasons the MED and the Larval Dynamics and Ecosystem Dynamics Investigations in particular will focus modelling efforts on the recruitment problem.

THE RECRUITMENT PROCESS

General Strategy

While much of the recent work done at NEFC points to the importance of predation mortality on juveniles as the key process in regulating recruitment, other causes and life stages cannot be ruled out entirely. In fact, it is very likely that different processes act to a greater or lesser degree and on different stages during the first year of life in different years. This means we must sample all first-year stages of a cohort in order to have appropriate empirical data for clarifying mortality mechanisms and testing hypotheses. Another important aspect of our strategy is that the pace of model development should be linked to the level of understanding of the processes. In the case of GEORGE we tried to go too far too fast with inadequate knowledge of controlling processes, and we generated unrealistic expectations of predictive capability. This time we intend to use the models initially to help evaluate and describe the processes, and then begin to develop predictive models. We intend to devote sufficient resources for a thorough analysis of all the data available and relevant data archives as well as collect critical new data in order to gain adequate insight into controlling mechanisms.

We will construct several research models (small in comparison with GEORGE) that will be designed to test various hypotheses about the recruitment process. These models and the associated analytical work will be an integral part of the proposed field and laboratory studies on the first year of life for target species, as described in the MED recruitment initiative. These models will be developed to take advantage of the dynamic model processor (DMP) developed by John Hauser. Using the DMP will make it easier to code the models as the processor takes care of all the input-output chores. Perhaps more importantly, using the DMP will enforce a certain amount of standardization which will make it much easier for other modelers within the Center to use and evaluate the models.

Retrospective Analyses

We intend to carry out a comprehensive series of retrospective analyses on various physical and biological factors and recruitment success for species with long time series (e.g. Sissenwine et al., 1980; Cohen et al., 1982; Koslow, submitted; Edwards, 1984). In particular we intend to carry out a detailed regression analysis of recruitment variability for major species for the years 1977 to date when we have had intensive MARMAP coverage, analyzing abundance and distribution of larval, and juvenile stages and their predators in relation to the physical environment and to recruitment success. Haddock, cod and yellowtail (principal target species of our recruitment initiative) would be analyzed as well as mackerel, silver hake and herring (ICNAF series). These retrospective studies will help clarify the degree of linkage between recruitment and various possible mechanisms to be included in the model.

Field and Laboratory Studies

In order to adequately test hypotheses about the relative importance of predation mortality on juveniles of target species, additional data will be necessary on the various life stages within the first year of life, including abundance of eggs, larvae and juveniles at least to age 9 months, and studies on growth, condition and feeding. These data will be needed to document variations in the timing and magnitude of mortality, and whether growth rate and condition (RNA/DNA, parasite load, etc.) are related to mortality. Estimates of the distribution and abundance of the predator field, and the food consumed by the various predators (particularly those that prey on juveniles of the target species) is also required, to determine the extent to which variations in juvenile mortality can be explained by predation.

Physical oceanographic studies on the re-circulation of water on Georges Bank vis á vis the life history of the target species will also be a part of our recruitment initiative including the construction of the models. Physical parameters that should be considered include temperature, stratification, current pattern (movement of water onto, around and off Georges Bank), and vertical shear in the flow field (this for looking at behavioral mechanisms).

The studies outlined above are all necessary to evaluate the mechanisms to be modelled as well as to provide the appropriate data for the models. It is important that these preliminary studies and data collection be carried out in close cooperation at all stages between the modelers and the field and laboratory scientists involved in the recruitment task force.

Recruitment Modelling

Concurrent with the above investigations we will be constructing a series of research models for the target species, haddock, cod, and yellowtail flounder; for example, the larval growth and survival model of Laurence (1983). These models will incorporate a detailed model of the first year of life, starting with the egg stage. The growth and survival of the cohort will then be followed for twelve months. Mechanisms that will be included in the model are size selective predation modified by the ecology of the predators and prey (e.g. spatial and temporal distribution of predators and prey, pathobiology, advection and recirculation of water on the Bank, and the effects of temperature on the growth and feeding of the target species and their predators).

These models will be run one year at a time starting from egg abundance. The number of eggs will come from either MARMAP survey data or be calculated from fecundity and stock structure. The number of eggs in the model can be made to follow a spawning curve so that the survival of eggs spawned at different times throughout the season can be followed. This may prove to be a key process in recruitment as recently it has been shown that in some years, the bulk of anchovy recruits are from one portion of the spawning curve, i.e., spawned either early or late in the season. Validation of the models with respect to the timing, magnitude and causes of mortality in the first year of life will be accomplished by comparing the abundance of model cod, haddock and yellowtail during the various stages of the first year of life with the actual larval and juvenile survey data in those years for which we have data. Using the insight from these analyses, additional testing will involve comparisons of the number of recruits predicted by the model with the actual number estimated by VPA (or trawl survey) for the much longer time series based on assessment data. We are also going to test the model by looking at the model food habits compared to the empirical food habits data base.

Different modelling projects would involve different aspects of the physical environment. Some specific examples (which do not include all possibilities by any means) might be: 1) The onset of larval hatching as related to the spring warming and the onset of stratification; 2) The distribution of larvae on the bank due to circulation of water about the bank; 3) Larval losses due to cross-shelf exchange processes (storms, warm core rings, etc.) on the southern side of the bank; 4) The recruitment of juveniles to the northern side of the bank due to recirculation of water on the bank; and 5) Large-scale shifts in the distribution of larval and juvenile predators due to the inter-annual variability of ocean and atmospheric climate.

There are two possible approaches to providing physical input to the model: 1) Derive the velocity fields and/or the distribution of hydrographic variables (temperature, salinity, and nutrients) from first principles; and 2) Specify the flow field mathematically and hydrographic patterns as they are known to exist on the bank from field measurements. These two approaches in fact have different goals: The first elucidates the physical factors responsible for the circulation on the bank, while the second provides a statement of conditions as they are known to exist, irrespective of how they are caused. The first approach, i.e. starting from first principles, involves solving the properly-formulated hydrodynamic equations with the correct boundary conditions in three-dimensions, a formidable task which must be done numerically since the relevant non-linear equations cannot presently be solved analytically. Considerable effort has already been expended on this approach by other groups, most notably Applied Science Associates, Inc. (Spaulding, Swanson, et al.) of Wakefield, R.I., and the Canadian school (Greenberg, Loder, Garrett, et al.) at Bedford Institute of Oceanography and

Dalhousie University. These people have dedicated fast computers and many man-years of effort to produce models that, while valuable, still do not produce all the known details of the flow. It should be noted that all the relevant aspects of the circulation on Georges Bank are not yet known (percentage of reçirculation and offshore volume transport by large storms, for instance) and our field programs will be continued to provide these important missing pieces of information. With this information we will reexamine the existing models with an eye towards validating them against the known circulation and applying them to specific recruitment hypotheses. For example, one area where a first principle approach may be useful is response of Georges Bank to severe storms (e.g. Beardsley and Haidvogel, 1981).

We think that the second approach is more likely to elucidate the linkages between the physical environment and recruitment, and it is the approach which can be most readily implemented within the Marine Ecosystems Division. Therefore, we will focus on the second approach, i.e. specify particular aspects of the Georges Bank flow field as known from existing and future field programs, as needed for input to the specific research models. This will be done in a timely way and include adequate variability to approximate the real conditions on the bank. Secondarily, we will work cooperatively with oceanographers outside NEFC on exploration and validation of the theoretical models. For example, we will carry out joint activities with Dr. John Paul and his group at EPA under our existing memorandum of understanding and also initiate joint modelling exercises with oceanographers at URI or WHOI as part of the joint NEFC-WHOI cooperative research agreement.

The research models will provide insight into the recruitment process which can then be used in a model like GEORGE, that will allow simulation for several years, with feedback from fishing as well as the environment on stock structure. We think this larger model can only be developed with confidence after the research models are tested and validated. The larger model may then be used to predict the potential long-term effects of various management strategies on the stocks on Georges Bank.

All of the above modelling activities focus on natural mortality factors for selected offshore target species on Georges Bank. Since Georges Bank is relatively free of contaminants, natural factors (including parasites and disease) can thus be assumed to be of primary importance. However in inshore areas, important target species such as striped bass and winter flounder are subject to contaminant effects which may very well be significant if not controlled. MED has unique expertise and facilties at Narragansett for investigating pollution effects on early life stages, and thus it seems appropriate for MED to play a significant role in the NEFC environmental assessment activity, and particularly within the context of the recruitment process. Both experimental and modelling capabilities are available and both need to be integrated for an effective approach to the problem. An outline of such a program and how it would be coordinated with other NEFC groups is given in a recent issue paper by Laurence (memo of 9 March).

Cooperating Researchers for Recruitment Modelling

The modelling effort will of necessity involve close working relationships with numerous researchers within the Division as well as in other divisions of the NEFC. The data on the abundance of eggs and larvae will come from the investigators of the Ichthyoplankton Investigation of W. Smith at Sandy Hook. Additionally, data on fecundity from W. Morse and others at Sandy Hook will be combined with data on the stock structure and fraction mature at age from the assessment, aging and survey groups at Woods Hole. G. Laurence's group in Narragansett, together with G. Bolz in Woods Hole, will provide data on larval growth and survival. Aging data on juveniles will be compiled by the age and growth unit in RAD and G. Bolz at Woods Hole.

The estimates of juvenile abundance will be made by the group under the direction of G. Laurence which includes G. Lough, D. Potter, J. Green and others in Narragansett and Woods Hole.

The retrospective analyses on physical forcings and recruitment will involve the physical oceanography group in Woods Hole (D. Mountain, R. Schlitz, S. Ramp) as well as AEG. Regression analysis of recruitment as the dependent variable vs. the independent variables of relative prey and predator abundance will be carried out with M. Pennington.

Determination of species groupings and predator fields will include the work by S. Murawski, W. Overholtz and W. Gabriel, and will be incorporated into the recruitment models to describe the ecological relationships between the target species and their prey. This includes overlap of predators and prey in space as well as grouping predators into functional units with similar predation characteristics. We also plan to work closely with the modelling group in the Assessment Division in formulating ideas about the recruitment process to be included in the model. The modelling effort will greatly benefit and be better able to contribute to the Center's recruitment studies if the modelling process and personnel are closely integrated with the field and laboratory studies supporting it as well as with the other modelling studies being carried out within the NEFC.

Investigation of parasite and disease conditions would be achieved through coordination with the Pathobiology Division (Oxford). Research on pollution effects on early life stages would be a cooperative effort involving the Larval Dynamics Investigation of MED and the Physiological Effect of Pollution Stress Investigations of the Environmental Assessment Division at Milford.

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